

This is the peer reviewed version of the following article: Pellegrini, A. F. A., Anderegg, W. R. L., Paine, C. E. T., Hoffmann, W. A., Kartzinel, T., Rabin, S. S., Sheil, D., Franco, A. C. and Pacala, S. W. (2017), Convergence of bark investment according to fire and climate structures ecosystem vulnerability to future change. *Ecol Lett*, 20: 307–316, which has been published in final form at <https://doi.org/10.1111/ele.12725>. This article may be used for non-commercial purposes in accordance With Wiley Terms and Conditions for self-archiving.

# Convergence of bark investment according to fire and climate structures ecosystem vulnerability to future change

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**Running title:** Fire tolerance in savanna and forest biomes

**Keywords:** fire ecology, functional traits, bark thickness, global change, savanna, forest

**Data accessibility:** Unpublished trait data will be made available in Dryad.

**Type of article:** Letter

**Statement of authorship:** AFAP and WRLA conceived of and designed the study. AFAP performed analyses with input from WRLA, TK, CETP, and SWP. WAH, SSR, CETP, DS, ACF contributed data. AFAP wrote the first draft of the paper and all authors contributed comments.

**Words/Figures:** Main text: 5,473; Abstract: 150; 4 figures; 0 tables; 50 references

Accepted for publication in *Ecology Letters*, published by Wiley-Blackwell.

## 1   **Abstract**

2   Fire regimes in savannas and forests are changing over much of the world. Anticipating the  
3   impact of these changes requires understanding how plants are adapted to fire. Here we test  
4   whether fire imposes a broad selective force on a key fire-tolerance trait, bark thickness, across  
5   572 tree species distributed worldwide. We show that investment in thick bark is a pervasive  
6   adaptation in frequently burned areas across savannas and forests in both temperate and tropical  
7   regions where surface fires occur. Geographic variability in bark thickness is largely explained  
8   by annual burned area and precipitation seasonality. Combining environmental and species  
9   distribution data allowed us to assess the vulnerability to future climate and fire conditions:  
10   tropical rainforests are especially vulnerable, whereas seasonal forests and savannas are more  
11   robust. The strong link between fire and bark thickness provides an avenue for assessing the  
12   vulnerability of tree communities to fire and demands inclusion in global models.

## Introduction

How plant communities respond to perturbations imposed by novel fire regimes is an important uncertainty in predicting the reaction of ecosystems to future global change (Cochrane *et al.* 1999; Westerling *et al.* 2006). Increased burning in ecosystems that rarely experienced fire historically, such as moist tropical forests (Nepstad *et al.* 1999), can result in rapid ecosystem degradation due to the lack of woody plant species with fire-tolerance traits (Uhl & Kauffman 1990; Cochrane *et al.* 1999). The loss of woody plant biomass during fires produces substantial carbon emissions (van der Werf *et al.* 2010), and may act to accelerate climate change, which is critical given projections of increasing fire occurrence in future climates (Moritz *et al.* 2012). Consequently, predicting the future of the terrestrial carbon sink depends on the ability of ecosystem models to accurately capture the fire tolerance of woody plants to future fire regimes (Huntingford *et al.* 2008).

Fire can be a strong selective force, and many tree species have evolved traits to better tolerate frequent burning and intense fires (Simon *et al.* 2009; Rosell *et al.* 2014). Variability in plant traits related to fire tolerance can determine the response of ecosystems to fire (Rogers *et al.* 2015), thus requiring a need to understand both the current distribution of traits as well as the mechanisms that generate their variability. The evolution of fire tolerance traits within numerous and widely distributed plant species and clades may allow communities containing those taxa to be more robust to increasing fire frequency (Pellegrini *et al.* 2016). Alternatively, if the global distribution of taxa that have evolved fire tolerance traits is limited to specific biomes or plant lineages, then some communities may be especially vulnerable. Consequently, understanding the mechanisms leading to the evolution of fire tolerance traits will give insight into potential constraints on the capacity of ecosystems to respond to changes in fire regimes.

In addition to the vulnerability of individual plant species, the distribution of fire tolerance traits in a community is important for determining vulnerability of an ecosystem to increased burning. On short timescales (i.e., years to decades), the potential for loss of woody plant biomass and carbon storage is determined largely by the vulnerability of individuals present in a community (Uhl & Kauffman 1990). Variability in the distribution of fire tolerance traits within a plant community is important, however, as it determines the overall proportion of plant species vulnerable to intensifying fire regimes as well as the potential for fire-tolerant species to replace fire-sensitive ones (i.e., ecological filtering; (Cavender-Bares & Reich 2012)). Moreover, trait-environment relationships can reveal how environmental conditions may filter species according to their traits, providing insight into the vulnerability of communities to change (Diaz *et al.* 1998). Consequently, we can estimate the ability of plant communities to tolerate increased burning by combining knowledge on the present-day distribution of fire-tolerance traits with projections of future fire regimes.

Here we examine global patterns of a key woody plant trait, bark thickness, which confers fire tolerance for trees in ecosystems with surface fire regimes such as xeric pine and oak forests (Harmon 1984); rainforests (Brando *et al.* 2012); savannas (Hoffmann *et al.* 2009; Lawes *et al.* 2011)). Bark is important because it helps protect the stem from overheating during a surface fire, conferring resistance to losses of aboveground biomass through either complete mortality or topkill. Although other traits can also influence whether fire actually kills a tree, such as the ability to resprout and location of buds inside the stem (Clarke *et al.* 2010; Pausas *et al.* 2016), bark thickness has been shown in numerous studies across multiple ecosystems (Harmon 1984; Van Nieuwstadt & Sheil 2005; Hoffmann *et al.* 2009; Brando *et al.* 2012; Pellegrini *et al.* 2016) to be a critical trait for the vulnerability of plant bole biomass – the largest

carbon storage pool in trees – to fire (explaining the majority of the variability in biomass losses with  $r^2 \geq 0.80$ ). Crown fire regimes are also important for a number of ecosystems, where plants contain a suite of other adaptations to either resist crown char (by growing tall and dropping branches) or quickly re-grow after a stand-replacing fire (through adaptations like serotinous cones, e.g., (Rogers *et al.* 2015)). However, here we focus on ecosystems with surface fire regimes.

We examine patterns of bark thickness to better understand ecosystem vulnerability to fire by addressing three questions: (i) how does bark thickness differ across species in different biomes and regions? (ii) to what degree do differences in fire frequency and fire-climate interactions filter species' relative bark thickness? and (iii) based on current bark thickness distributions and projected changes in climate and fire, how does the vulnerability to future fire regimes differ across savannas and forests worldwide? Although absolute bark thickness generally increases with stem size, plant species differ in their relative investment in bark. Consequently, we quantify bark investment as the thickness of bark at a standardized stem diameter (i.e., relative bark thickness).

## Methods

### *Dataset compilation*

We compiled a dataset of bark thickness investment across 572 abundant woody plant species distributed across biomes worldwide from published and unpublished sources (Table S1). To account for the influence of stem size and allometric equations reported (which varied from linear to saturating), we calculated bark thickness at three stem diameters —10cm, 20cm, and 30cm—which spanned the critical range of stem size over which trees are most vulnerable to

topkill and comprise a large proportion of tree biomass in savannas and forests (Uhl & Kauffman 1990). We also verified that our results were robust to alternative calculations of bark thickness (*Supplementary Information, SI*).

#### *Comparison among biomes and continents*

We classified species as being associated with savanna vs. forest biomes because these biomes have different fire regimes and woody plant species tend to specialize in either savanna or forest biomes, but not both (Hoffmann *et al.* 2012). Savannas are defined as ecosystems with intermediate tree cover (20-80%) and a continuous grassy layer while forests have complete woody cover and grasses are minimal to absent (Staver *et al.* 2011). Species were grouped as specializing on savanna or forest biomes based on how they were categorized by the paper authors. In all cases where we compare bark thickness between savanna and forest biomes, we are referring to the comparison of species classified as specializing on either biome.

It is more difficult to classify species and make generalizations of fire regime differences between biomes in temperate forests and savannas (here we focused on North America in particular) given that (i) species can occur in multiple habitats (e.g., savannas, woodlands, forests); and (ii) forests can also experience a range of fire frequencies. Consequently, we complement our analysis with a detailed dataset specific to North America (*SI*) that classifies species into multiple habitat types based on a synthesis of existing distribution data. This allowed us to further test (i) whether species associated with more open vegetation (savannas and woodlands) experience fires more frequently than those with closed vegetation (mixed woodlands and forests) and (ii) how species' bark investment varied across these habitats.

To evaluate the potential for crown fire regimes to influence our results, we took advantage of the tendency for many North American forests, especially those dominated by gymnosperms, to experience crown fires. Consequently, we investigate the potential role of exposure to crown fire in modifying the relationship between bark and fire by testing how angiosperms vs. gymnosperms differ in their bark investment and bark-fire relationships (*SI*).

Comparisons between species grouped into different biomes (and other habitat classifications in North America) were performed using ANOVAs, with the potential covariate interactions among biome, continent, and region (i.e., tropical vs. temperate locations) evaluated using ANCOVAs.

#### *Establishing environmental conditions for each species*

We determined the spatial distribution of species using field georeferenced locations from the Global Biodiversity Information Facility (GBIF) to obtain global occurrence data (Fig. S1). These distribution data were combined with burned area estimates and climate data to obtain the average environmental conditions over the distribution of each species. In all cases, the distribution of the mapped areas cover the complete ranges of all the included species. For fire, we analyzed two burned area datasets spanning 10 and 19 years, which are currently the longest available datasets on global fire patterns. This assumes that relatively recent spatial patterns of fire frequency structure patterns in bark thickness. The first fire dataset is the annual burned area product from the Global Fire Emissions Database 3 with small fires (spanning 2001-2010) (hereafter referred to as GFED3s), which aims to account for detection of fires in closed-canopy forests (Randerson *et al.* 2012; Giglio *et al.* 2013). The second is the annual burned area product from GFED4, which spans 1997-2015, but does not yet have the correction for small fires. We



focus our analyses on the shorter time-series GFED3s because the systematically lower measured frequency of fires in forests in GFED4 (*SI*) likely misses the key role of small fires in forest areas. Nonetheless, our results are qualitatively consistent when using the longer GFED4 record (*SI*).

Here we were concerned with the climate factors that have the potential to influence fire behavior. Consequently, we focused on precipitation partitioned into the driest and wettest quarter obtained via WorldClim (Hijmans *et al.* 2005). Higher precipitation in the driest quarter can increase fuel moisture and thus reduce burned area and intensity. On the other hand, higher precipitation in the wettest quarter can increase fire intensity in biomes with grasses (which grow but then dry out, becoming highly flammable in the dry season (Govender *et al.* 2006)).

To determine the relative impact of fire, climate and the interaction between climate and biome on relative bark thickness, we performed model selection on generalized additive models using the lowest Akaike Information Criterion (AIC), with a threshold of two. Model selection was used to assess variable importance as well as the potential for non-linear relationships. We focus on the results for 10cm, but results from other stem diameters are presented in the *SI*, all of which yielded qualitatively similar results. Bark thickness and annual burned area were log-transformed prior to analysis to reduce heteroscedasticity.

#### *Comparison across taxonomic groups*

We used linear mixed-effects models to compare the bark thickness of savanna and forest species nested within their corresponding genera and families, using either family or genus as random effects. Consequently, this analysis is only performed on the species where both savanna and forest species are present in the same genus or family. We also performed a regression

between the mean bark thickness of savanna species and forest species grouped within each genus and family. This was used to determine whether the bark thickness of savanna species was correlated with the bark thickness in forest species.

#### *Vulnerability to future changes*

To estimate the vulnerability of plant communities to future changes in climate and fire, we aggregated individuals into 1°x1° gridcells across the globe using the GBIF distribution data to calculate mean bark thickness values for each gridcell (incorporating the abundance of individuals within a species and the bark thickness for that species). We performed this aggregation process separately for savanna and forest species because of the potential biome-by-climate interaction. We refer to these spatially aggregated values as the “community” bark thickness. Climate and burned area data were also calculated for each gridcell. We fit a generalized additive model between bark thickness and environmental data across all gridcells for both savanna and forest communities (statistical fits and a verification that our results are robust to spatial autocorrelation are in the *SI*).

We then used the regressions between climate, fire, and community bark thickness to project the future expected distribution of bark thickness according to future fire and climate conditions. Future climate conditions were determined from five climatic models obtained via CMIP5 outputs for 2070 RCP8.5 scenario (*SI*). Future fire conditions come from a recent output of annual burned area from LPJ-GUESS-SIMFIRE (Knorr *et al.* 2015), which incorporates future climates, human populations, and fuel loads (*SI*), for 2071-2100 RCP8.5 scenario. We chose the high emissions scenario to quantify an upper bound on potential changes in fire regimes. We averaged forecasted values across all models within each grid cell. To evaluate

climate uncertainty, we used the standard deviation among climate model precipitation projections to calculate “wet” and “dry” (+1 vs. -1 standard deviation precipitation, respectively) future scenarios. The potential role of uncertainties in fire projections are presented in the discussion.

The robustness of communities to change was then quantified by comparing the current distribution of bark thickness within gridcells with the expected future distribution. Specifically, we used the log-transformed community means and variances to generate a normal distribution of bark thicknesses for each gridcell. Next, we used the projected community mean bark thicknesses to generate a normal distribution curve of future bark thickness for each gridcell, assuming that present day variances remained unchanged. The ability of a particular community to achieve the future expected bark thickness was quantified as the area under the two probability densities (Fig. S2), which is known as the overlapping coefficient (OVL, (Inman & Bradley 1989)). Here we interpret the OVL to be a measure of robustness because it estimates the fraction of individuals with bark thicknesses compatible with future conditions. Consequently, the OVL estimates the potential for an ecosystem to adjust to more extreme conditions through shifts in the abundance of its current species pool. Importantly, this metric estimates only the relative robustness of gridcells, it does not predict the percent of individual trees that will be lost.

## Results

Across the globe, investment in thick bark is a consistent adaptation to fire-prone environments. At the biome scale, bark was three-fold thicker in tree species specialized in fire-frequent savannas vs. fire-infrequent forests (Fig. 1, Tables 1,S2). This pattern was observed across Africa, Australia and the Americas, each of which contain extensive savanna-forest

boundaries (Fig. 1, Tables 1,S3), and was robust to variation in stem size and alternative calculations of relative bark thickness (Fig. S3, Table S3). We confirmed that savanna species differed broadly from forest species in their characteristic fire regimes using remotely sensed estimates of annual burned area from both the long time series ( $F_{1,569}=154.8$ ,  $p<0.0001$ ) as well as the shorter time series that corrects for small fires ( $F_{1,570}=187$ ,  $p<0.0001$ ).

Within the broad global pattern, the differences in bark thickness between species specialized in savanna vs. forest differed in magnitude across regions and continents (Figs. 2,S4,S5, Tables S2-S4). In the tropics, savanna species had 3.3-fold thicker bark than forest species, while in temperate regions this difference was only 1.4-fold (Table S2), consistent with the greater between-biome differences in the fire frequency characterizing species' distributions in the tropics (Fig. 2).

Among continents, there was substantial variability in the bark thickness of species both in the savanna and forest biomes (continent-by-biome interaction:  $F_{4,562}=15.6$ ,  $p<0.0001$ , Figs. 1,S5, Tables S2,S4). As a result, Australia and South America had the starkest contrast between biomes, with savanna species having 5.3- and 3.8-fold thicker bark than forest species, respectively (Figs. 1,2,S5, Tables S2,S4). On the other hand, North American and African savanna species were only 1.4- and 1.8-fold thicker than forest species (Figs. 1,2,S5, Table S4). Only in Asia did we not find a significant difference between biomes (Table S3), although there were data on only a few savanna species ( $n=5$ ). Consistent with the continent-by-biome interaction for bark thickness, we also found a significant interaction for fire frequency ( $F_{4,562}=4.54$ ,  $p=0.0013$ ). Subsequently, the contrast in bark thickness between savanna and forest species was largely consistent with the contrast in fire frequencies that characterized their distributions (Fig. 2); we quantitatively test for the relationship between bark and fire below.

A more detailed evaluation of the habitat preferences of species in North America revealed qualitatively similar results: species that predominantly occurred in savanna habitats experienced a higher frequency of burning than those found only in forests (GFED3s:  $F_{2,74}=9.15$ ,  $p=0.0002$ , GFED4:  $F_{2,74}=10.75$ ,  $p<0.0001$ ); correspondingly, species that predominantly occurred in savannas tended to have 1.4-fold thicker bark than those found only in forests ( $F_{2,74}=4.1$ ,  $p=0.020$ ), in spite of North American forest species experiencing relatively frequent burning (*SI*, Fig. S6).

Globally, variation in bark thickness across species could be explained by the fire regime, climate, and the interaction between climate and fire that characterized a species' distribution. First, annual burned area alone explained 20% of the global variation in bark thickness, with bark thickness increasing as a nonlinear function of the annual burned area that characterized a species' distribution (Fig. 3A, Table 1). Second, species found in areas with lower dry season rainfall tended to have thicker bark in both savannas and forests (Fig. 3B, Table 1), likely a result of the negative relationships between dry season moisture and annual burned area ( $t = -3.726$ ,  $p<0.001$ ) and fire intensity (Govender *et al.* 2006). Third, there was a significant interaction between precipitation in the wet season and the biome a species specialized on; bark thickness of savanna species increased with wet-season precipitation whereas that of forest species decreased (Fig. 3C, Table 1). This climate-biome interaction likely reflects adaption to the higher fuel loads and more intense fires in the more productive wetter savannas, which our remote sensing fire metric cannot capture but has been well established across savannas (Williams *et al.* 1999; Govender *et al.* 2006). All conclusions were robust to variation in stem diameter (Table S5) and the different burned area products (Fig. S7, Table S6,S7). AIC-based model selection illustrated that the most parsimonious model included annual burned area and

biome-precipitation interactions and explained 50% of the deviance in bark thickness across all 572 woody plant species (Table 1).

The potential for crown fire regimes to influence our results was explored by evaluating bark-fire relationships across plant communities in North America, under the assumption that gymnosperm forests have a higher probability of experiencing crown fires and may invest less in bark. Across all species, fire frequency appears to be a less powerful, but still significant, predictor of bark thickness (explaining 7.6% of deviance across species, Table S8). Comparisons between gymnosperm and angiosperm species illustrated no significance difference in bark thickness between groups when we considered either all species or only forest species (*SI*). However, when gymnosperms were analyzed alone, we found that the significant relationship between bark and fire frequency depended on the habitat of a species ( $F_{1,24}=5.16$ ,  $p=0.032$ ), with no relationship between fire and bark in species that occurred only in forests. Consequently, the relationship between fire frequency and bark becomes less significant in habitats prone to crown fires.

Comparisons among congeneric species and species within the same family illustrated that bark thickness is well matched to the environment across diverse plant lineages. At the genus level, species associated with the savanna biome had 2.07-fold thicker bark than their congeneric forest species ( $n=32$  genera, 156 species,  $t=8.46$ ,  $p<0.0001$ ; Fig. 4A). At the family level, savanna-associated species had on average 2.59-fold thicker bark than forest-associated species in the same family ( $n=36$  families, 377 species,  $t=20.52$ ,  $p<0.0001$ ; Fig. S8). Moreover, there was no significant relationship between the bark thicknesses of forest species and the savanna species within either shared genera or shared families ( $r^2<0.01$ ,  $p=0.29$  and  $r^2<0.01$ ,  $p>0.5$  respectively; Fig. 4B,C), illustrating that the investment in bark of a savanna species is

independent from the investment in bark of a forest species within shared clades (i.e., thicker barked savanna species are not significantly more likely to come from thicker barked forest species and vice versa).

Fire frequency is expected to increase in many areas that currently contain savanna and forest species. Specifically, 61% and 63% of savanna- and forest-containing grid cells are expected to experience increases in the proportion of area burned each year, respectively, in a high emissions climate scenario (Fig. 5A). However, the robustness of plant communities is forecasted to vary widely among biomes. Communities of savanna species have higher robustness than forest communities, on average, despite having higher fire frequencies and experiencing equivalent relative gains in annual burned area (Figs. 5,S9). Accordingly, the distribution of robustness across grid cells reveals that 93% of savanna gridcells had >50% of individuals with traits consistent with future fire conditions whereas only 62% of forest gridcells exceeded the threshold of 50% (Fig. S9C). The qualitative trends were consistent regardless of different precipitation scenarios, although on average forest communities tended to be less robust under the “dry” scenario (only 55% of cells exceeded the threshold of 50%) and more robust under the “wet” scenario (63% of cells exceeded the threshold of 50%), while savanna community showed little change (both scenarios ~93% of cells above the threshold).

Variability in the potential robustness across regions identified sensitive areas, such as moist tropical forests and temperate forests in western North America, which have the lowest forecasted robustness. However, some areas of forest in western North America and transitional tropical forest at savanna-forest ecotones in South America have relatively high robustness (Fig. 5C,D), perhaps due to the historical presence of fire in these contrasting forests having selected for thicker barked species (Harmon 1984; Paine *et al.* 2010). Importantly, this analysis of

vulnerability is to surface fire regimes, and further analysis of the western North American forests that can experience crown fires in addition to surface fires is warranted. Tree communities in savannas tend to be robust because of the presence of thick-barked species that can persist even with increased annual burned area.

## Discussion

Convergence of thick bark as a fire tolerance trait reflects consistent filtering of species with thin bark from areas prone to surface fires. The physics that govern how fire kills a tree are consistent across biomes: the insulation provided by bark protects the tissue inside the stem from overheating. As a result, the negative relationship between bark thickness and the loss of aboveground stem biomass in a fire is remarkably similar across ecosystems (Uhl & Kauffman 1990; Lawes *et al.* 2011) and is even present in forests that can also experience crown fires such as those in western North America (Harmon 1984). Consequently, plant lineages distributed across the seed plants contain a broad range of bark thicknesses, and species that occur in historically fire-prone environments consistently exhibit high bark thickness, a pattern consistent with the convergent evolution of bark as a fire-tolerance adaptation.

The general relationship between frequent fire and investment in bark identified here is a substantial step forward, given that a recent review concluded the paucity of data on bark investment across species limits generalizability (Pausas 2015). Indeed there has been debate on the role of fire and potential climate-fire interactions in determining species' investment in bark (Hoffmann *et al.* 2012; Poorter *et al.* 2014; Rosell 2016). We help resolve this debate by illustrating the substantial role of fire and fire-climate interactions in determining global patterns of bark investment (Figs. 1-3). Additional explanations for variability in bark investment such as



defense against pathogens and mechanical stability are likely to contribute to the variability in the relationship between bark investment and fire (Paine *et al.* 2010; Rosell *et al.* 2014). These alternative factors may explain the result in Asia, where we did not find a significant difference in bark thickness between savanna and forest species. Nonetheless, our relatively simple model predicts 50% of the variance in bark thickness, illustrating the predominant role of fire in structuring the distribution of bark and presenting a framework to gain inference into how certain ecosystems differ in their vulnerability to future fire regimes.

Our approach to characterize the climate and fire niches of species using available distribution data allowed us to complement our between-biome analysis with continuous estimates of fire regimes. The consideration of continuous variability in climate and fire illustrated that a substantial amount of the variance among regions within biomes is due to their different fire and climate conditions. The variability in fire frequency and climates that exists across savanna and forest biomes (Lehmann *et al.* 2014) may explain why studies find inconsistent evidence on the degree to which thick bark is an adaptation to frequent fire (Hoffmann *et al.* 2009; Pausas 2015; Rosell 2016). For instance, even within savannas, species' investment in bark increased in areas with more frequent fire and higher wet quarter rainfall (Fig. 3B,C). This climate-fire interaction provides one explanation for the relatively greater investment in bark found in the wet South American savannas relative to the drier African savannas (Dantas & Pausas 2013).

North America presents a number of interesting contrasts to observations from the tropical savanna-forest ecotones. Many forest species in North America experience relatively frequent fires (Fig. S6), likely leading to their higher investment in bark relative to forest species in tropical forests in Australia and South America (Fig. S4). The comparable fire frequencies in

savannas and forests in North America is likely to contribute to the small differences in bark thickness between savanna vs. forest congeners in *Pinus* and *Quercus* (Fig. 4A,S8). Moreover, although we found that the bark-fire relationships were robust in North America where many species experience mixed fire regimes, gymnosperm tree species, which occur in habitats more likely to experience crown fires had a weaker relationship between bark and fire. Specifically, the bark thickness of gymnosperm forest species was not significantly related to fire frequency, which supports the hypothesis that other traits such as reseeding and resprouting are critical in crown fire ecosystems (Keeley *et al.* 2011). Consequently, consideration of other traits will be important for predicting the vulnerability to crown fires and presents a useful expansion to our current study that focused on surface fires.

We predict striking differences in robustness across biomes and regions, identifying especially sensitive areas in carbon-dense forests of the wet tropics where increases in fire activity are forecasted to occur throughout a large area where trees invest relatively little in bark (Fig. 5). In contrast, trees in drier tropical forests and the ecotonal areas between savannas and forests invest more in bark (Fig. 3B,C) and are better suited to tolerate the intensifying fire regimes (Fig. 5). Consequently, important heterogeneity exists across forests in different climates not just due to projections in fire activity, but the distribution of species with fire tolerance traits.

More accurate predictions of vulnerability will be gained as we reduce the uncertainties in the factors driving changes in fire. The future fire projection utilized here identified that assumptions about population growth heavily influence the projections of burned area; however, the direction of the projected fire trends across the areas that we identify as most vulnerable (e.g., moist Neotropical forests) were robust to different population growth and urbanization scenarios, even though the exact change differed (Knorr *et al.* 2016).

Further insight into mechanisms structuring variability in the vulnerability of ecosystems can be gained by considering other fire-tolerance traits such as resprouting or reseedling from serotinous cones (Ondei *et al.* 2015) that can allow thin barked species to persist in areas frequently burned (Bond & Midgley 2001). Nonetheless, by considering the full trait-environment probability distribution, our models of robustness partially account for the possibility that other traits may modify the relationship between the bark thickness of a species and the fire frequency it experiences. For example, the presence of thin barked species in a frequently burned area, which may be due to their capacity to resprout or rapidly reseed following a fire, will widen the estimated trait distribution and allow for greater variance in bark thickness at a particular fire frequency.

The ability to simulate the effects of fire on ecosystem carbon pools will depend on accurately capturing the distribution of traits within and across communities. Many Dynamic Global Vegetation Models, which are commonly used to forecast change in the global carbon cycle, use fire modules that represent fire tolerance traits as static properties of plant functional types, fixed within broad vegetation classifications (Thonicke *et al.* 2010; Li *et al.* 2012). We suggest that using a single bark thickness value per plant functional type fails to capture important heterogeneity in fire tolerance that exist within geographies and ecosystems and may allow for ecological filtering. Consequently, the use of fixed trait means, rather than distributions, may underestimate robustness to fire and lead to large error in estimates of carbon emissions.

We show that the widespread convergence of a fire tolerance trait, bark thickness, underpins a striking range of robustness exhibited by vegetation communities to future fire regimes. Estimates of ecosystem robustness can be further improved by considering additional

traits of the plant community, variation in the rates and mechanisms of trait evolution, other important disturbances such as drought. Nonetheless, trait-based approaches to assessing robustness to fire have the potential to be powerful predictors of the future response of ecosystems to fire.

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**Table 1:** Statistical results from generalized additive models between log bark thickness (for stems 10cm in size), fire, climate, and biome using model selection. Dev refers to deviance explained. Mean\_fire = annual burned area, Precip\_Wetq = precipitation in the wettest quarter, Precip\_Dryq = precipitation in the driest quarter, Biome = biome a species specialized in (either savanna or forest). The best fit models are highlighted in bold, we utilized the more parsimonious of the two.

<u>Variables included</u>	<u>Dev</u>	<u>AIC</u>
<b>Mean_fire+Precip_Wetq*Biome+Precip_Dryq*Biome</b>	<b>50.20%</b>	930
<b>Mean_fire+Precip_Wetq*Biome+Precip_Dryq</b>	<b>49.90%</b>	930
Mean_fire+Precip_Wetq+Precip_Dryq*Biome	47.40%	961
Mean_fire+Precip_Wetq+Precip_Dryq+Biome	46.50%	965
Precip_Wetq+Precip_Dryq+Biome	46.30%	966
Mean_fire+Precip_Dryq+Biome	44.80%	984
Mean_fire+Precip_Wetq+Biome	40.80%	992
Mean_fire+Biome	35.60%	1049
Biome	35.50%	1066
Mean_fire+Precip_Wetq+Precip_Dryq	30.20%	1065
Mean_fire	21.60%	1180

**Figure 1: Broad evidence for high bark investment in savanna environments.** Comparison of bark thickness, normalized to a 10 cm stem size, in plant species across the globe. Map was generated using an inverse distance weighted approach to create spatial averages of trait values from GBIF occurrence data within distances of 0.5° around each observation point. Dark grey areas indicate locations that do not contain species distribution/bark thickness data. Color ramp is pivoted on the median of bark thickness to illustrate relative variability across the globe. The box-plot comparisons between savanna and forest species are across four continents that contain extensive savanna-forest ecotones. Statistics and sample sizes are in Table S2.

**Figure 2: Difference between savanna and forest species across regions and continents.** Comparison of the ratio of the mean bark investment and fire frequency of savanna vs. forest species between regions (A) and among continents (B). In all cases the ratio is calculated by dividing the savanna value (averaged within either the region or continent) by the forest value. Significance of the interactions were determined by ANOVAs. A) Region-by-biome interaction for fire ( $F_{1,568}=26.4$ ,  $p<0.0001$ ) and bark thickness ( $F_{1,568}=26.0$ ,  $p<0.0001$ ). B) Continent-by-biome interaction for fire ( $F_{4,562}=4.54$ ,  $p=0.0013$ ) and bark thickness ( $F_{4,562}=15.6$ ,  $p<0.0001$ ). For specific comparison among continents, see Table S4.

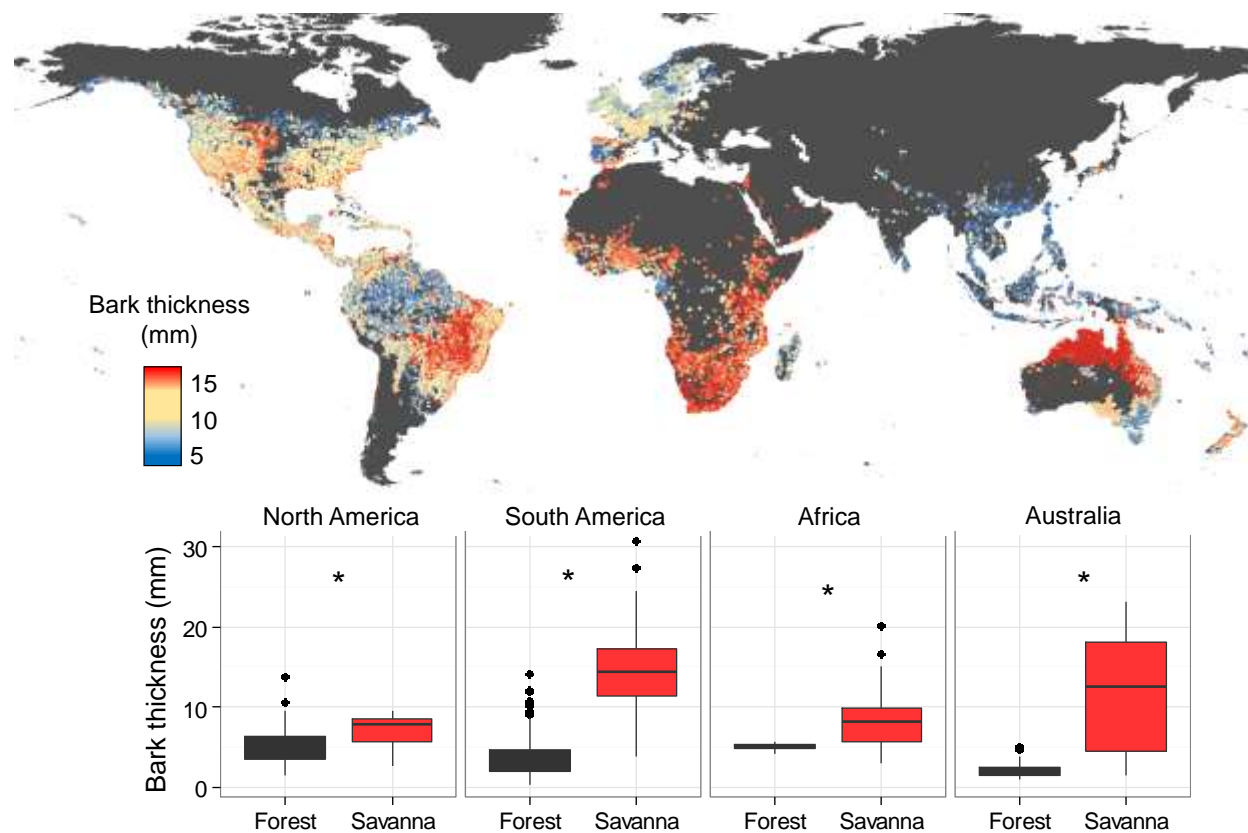
**Figure 3: Key role of environment in determining the relative bark thickness of plant species.** A) Relative bark thickness of a species vs. the mean annual burned area of a species' distribution across all species on log-transformed annual burned area and bark thickness data. Solid line represents model fit. Appropriate nonlinear fit determined using model selection (nonlinear fit AIC=1180, linear fit AIC=1209). Bark thickness of savanna and forest species vs. mean climate of a species' distribution for precipitation in the driest quarter (B) and wettest quarter (C), solid line indicates fitted model relationship with the dashed lines indicating 95%

confidence intervals. Separate lines were fitted in (C) because of the significant climate-biome interaction. The complete model of annual burned area, precipitation, and biome explained 50% of variation in bark thickness.

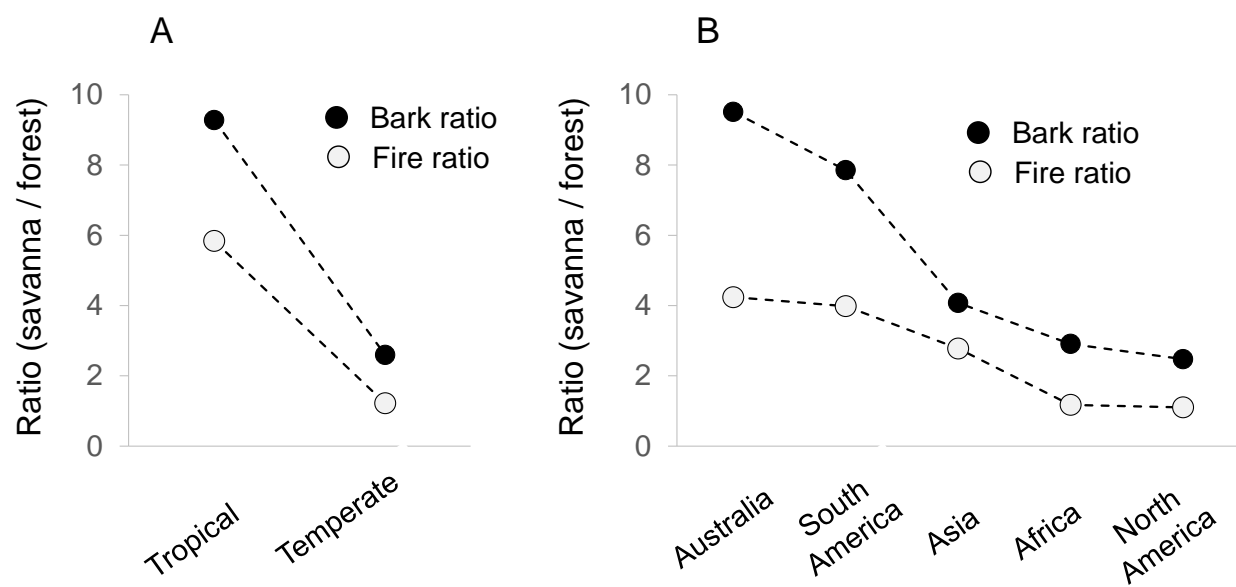
**Figure 4: Savanna species have consistently thicker bark than their congeners. A)**

Comparison of bark thickness in species specializing in savannas vs. forests in the same genus across 32 genera containing 156 species. Scatter plots comparing the bark thicknesses of savanna vs. forest species within each genus (B) and family (C). Error bars are  $\pm 95\%$  confidence intervals. The dashed line illustrates a 1-to-1 line.

**Figure 5: Heterogeneity in robustness.** Global distribution of future fire regimes and the overlapping coefficient (OVL) comparing the difference in probability distributions of bark thicknesses between present day and future conditions. A) relative change in annual burned area, expressed as the % of a gridcell burned, between the present day (based on 2001-2010 observations) and the future (projections to 2070-2100). B) forecasted annual burned area for year the 2070-2100 period. C-D) OVL between present day and future trait distributions for forest (C) and savanna (D) communities. The spatial overlap of colored points in panels C and D results from the spatial proximity of savanna and forest biomes in those gridcells. Only gridcells projected to experience gains in fire frequency are mapped in panels C and D.

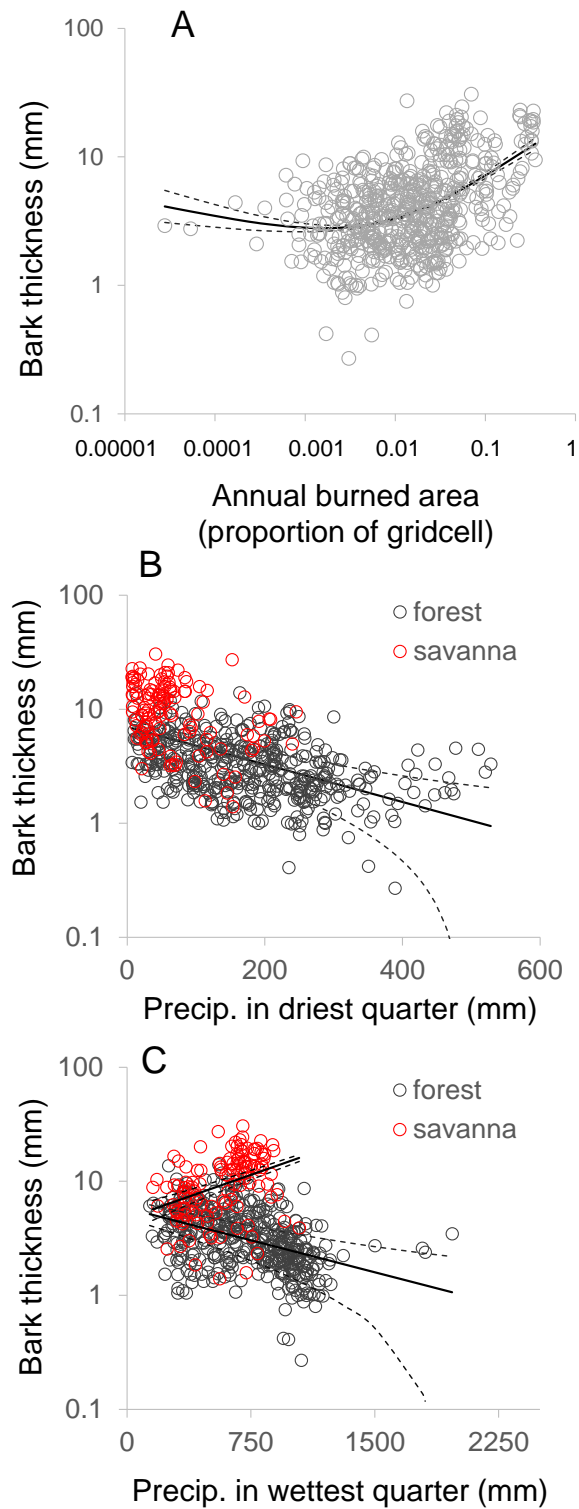
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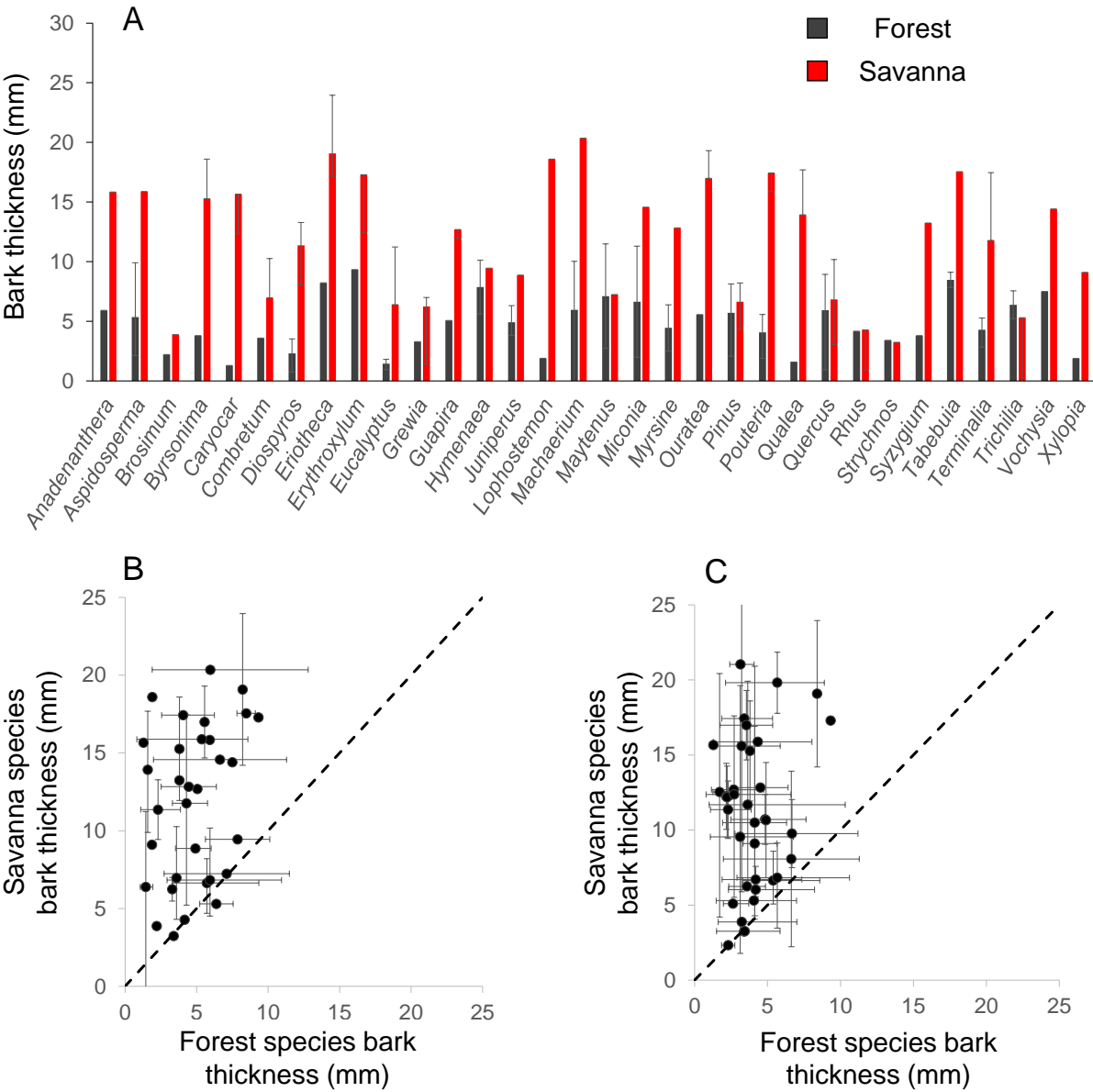
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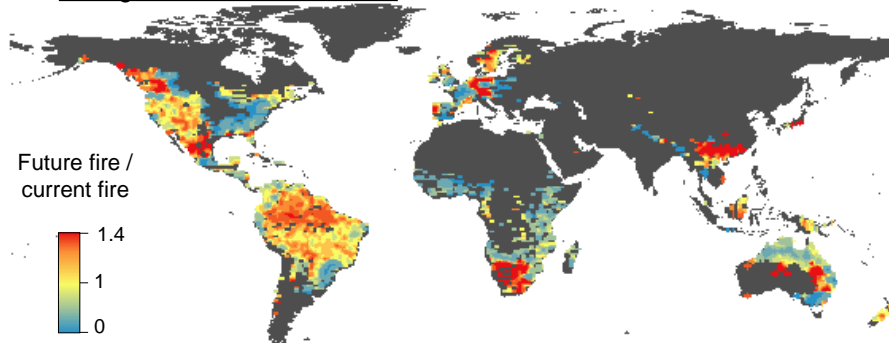
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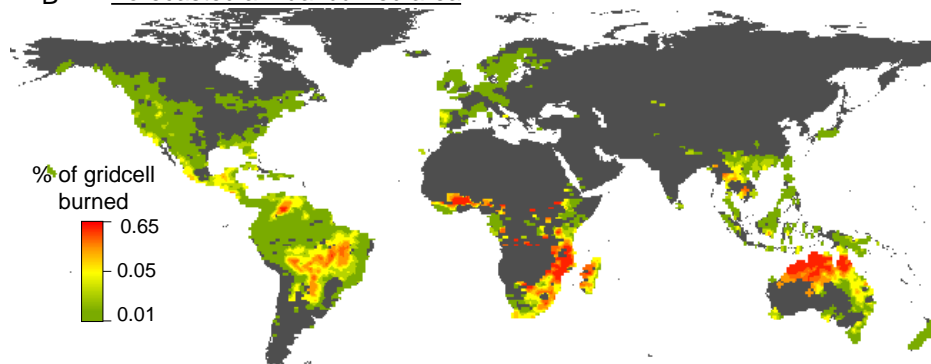


610 **Figure 5:**

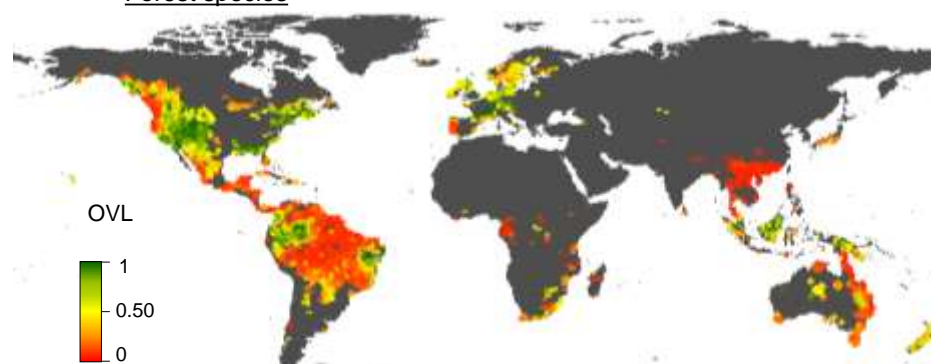
A Change in annual burned area



B Forecasted annual burned area



C Forest species



D Savanna species



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## Supplemental Information

### Different stem allometries and calculations

Because absolute bark thickness is positively associated with stem diameter, and published studies have used different allometric equations to relate stem diameter with bark thickness, we calculated bark thickness for identically sized trees to allow for comparability. We calculated bark thickness at three stem diameters—10cm, 20cm, and 30cm. These diameters span the critical range of stem size over which trees are most vulnerable to topkill and comprise a large proportion of tree biomass in savannas and forests (Uhl & Kauffman 1990; Barlow *et al.* 2003; Pellegrini *et al.* 2016). The consistency of our results across these stem diameters illustrates our results are robust to the number of different allometric relationships (power, linear, logarithmic, etc.) both across and within studies.

Here, we calculate bark thickness based off of relationships determined between bark thickness and the stem diameter measured on the outside of the bark. One alternative way to calculate relative bark thickness is to relate bark thickness with the bole diameter of a stem (the diameter inside of the bark) (Midgley & Lawes 2016). We verified our results were robust to consideration of the ratio between bark and bole diameter by back calculating the bole diameter and calculating bark thickness on stems that were 10cm in bole diameter (we chose 10cm, because that is the primary size of our analysis). We found that in general bark thickness estimated from bole diameter was higher than from the outer bark, which tended to increase in thicker barked species (Fig. S3). However, the majority of our points have litter residual error and a partial re-analysis of the data illustrate that our qualitative results are not sensitive to whether bark thickness is calculated by outer stem size or bole stem size (Fig. S3).

### Establishing differences in fire frequencies between biomes

Using data on fire from a longer time-series (GFED4, 1997-2015), we found that savanna species experienced a 9.2-fold higher frequency of burning than forest species, expressed as the average proportion of a grid-cell that burns each year ( $F_{1,569} = 154.8$ ,  $p < 0.0001$ ). The shorter fire time-series (2001-2010) corroborated these results as savanna species experienced a 5.4-fold higher frequency of burning than forest species ( $F_{1,570} = 187$ ,  $p < 0.0001$ ) but also illustrated the potential that the longer fire product is biased against detecting fires in forests relative to savannas (inter-biome differences were twice as high when there were no corrections for small fires). Moreover, using GFED4, one species was categorized as experiencing no fire, likely due to the lack of small fire correction. Consequently we utilize the shorter time series to avoid detection bias in forests.

### Analyses in North America

We complemented our analysis with a more detailed dataset specific to North America from the Fire Effects Information System (USDA, <http://www.feis-crs.org/feis>) that classifies species into multiple habitat types based on a synthesis of existing distribution data and knowledge. The FEIS is a searchable database of fire regime characteristics and habitat associations for plant species that occur in North America. Because habitat categorizations were descriptive (and not quantitative), we developed our own classification scheme to best determine savanna vs. forest species. This involved categorizing species as associating with (i) only forest habitats, (ii) >90% forest habitats, (iii) mixed between forest and woodlands/grasslands/prairie/savanna, (iv) predominantly in woodlands/grassland/prairie/savanna. We then repeated our analyses comparing the two disparate categories as forest vs. savanna as well as the “mixed”

species. This allowed us to further test whether our assumption that species associate with more open vegetation (savannas and woodlands) experience fires more frequently than those with closed vegetation (mixed woodlands and forests).

Incorporating newly classified species as savanna vs. forest specialists using the detailed habitat dataset yielded quantitatively similar results in our comparison between savannas and forests in North America (savannas species had 1.31-fold thicker bark in original classification vs. 1.37-fold thicker bark in detailed classification).

We also used comparisons within North America to estimate potential effects of crown fire regimes influencing our results. Under the assumption that other traits such as reseeding, resprouting, and/or height allometry are more important than bark thickness, we would expect the relationship between fire and bark to be weak. Although we found that fire frequency was still a significant predictor of bark investment, fire only explained 7.6% of the deviance across species (Table S8), which is  $\sim 1/3$  of its explanatory power in the global analysis (21.6%). Model selection illustrated two models that were within 2 AIC of one another. The model that explained the most deviance included fire frequency, precipitation in the driest quarter, and habitat (19.7% of variance explained). Consequently, fire frequency appears to be a less powerful, but still significant, predictor of bark thickness.

Gymnosperm dominated forests in North America tend to be the forest types most prone to crown fires. Consequently, we compared the relative bark thickness of gymnosperm vs. angiosperm plant species as another indirect test of how crown fire regimes may be influencing the selection for bark thickness. We found no significant difference in relative bark thickness between gymnosperm vs. angiosperm tree species either across the entire dataset ( $F_{1,59}=1.8, p=0.184$ ) or within the subset of species that occurred primarily in forests ( $F_{1,39}=1.0$ ,

p=0.32), suggesting that different fire regimes may not influence the bark relationship heavily. However, we found no significant relationship between bark and fire frequency when we analyzed gymnosperms alone ( $F_{1,26}=1.9, p=0.18$ ). Further analysis revealed that the lack of a relationship between fire and bark thickness was dependent on the habitat of a species (fire\*habitat interaction,  $F_{1,24}=5.16, p=0.032$ ); in other words, the relationship between fire and bark was weak in species that occurred only in forests and stronger in species that occurred in savannas. Consequently, species that occur in habitats more likely to experience crown fires have a weaker relationship between bark and fire, under the assumption that gymnosperm forests are more susceptible to crown fire than angiosperm forests or savannas.

#### Statistical relationship between bark thickness, climate, and fire frequency

Incorporation of GFED4 to determine the fire frequency of species' distributions resulted in no significant qualitative changes to our model fit and selection analysis (Tables S6,S7).

In all cases, we performed model selection to determine the most parsimonious combination of variables (using the lowest AIC with a threshold value of two). We tested for potential non-linear relationships between variables by comparing the AIC of non-linear and linear fits. Analyses were performed separately for bark thickness on standardized diameters of 10, 20 and 30 cm, all of which yielded qualitatively similar results. Bark thickness and annual burned area were log-transformed prior to analysis to reduce heteroscedasticity.

#### Congener comparison

We removed the *Acacia* genus given the taxonomic issues as well as those with species that occurred in fundamentally different habitats (e.g., *Melaleuca* forest trees specializing in swamps).

#### Quantifying within-species variability in bark thickness allometries

To assess whether within-species variability in bark thickness could impact our conclusions, we evaluated the error within bark thickness allometry relationships across the studies that presented goodness of fit measures. An analysis of the goodness of fit between stem diameter and bark thickness illustrated low error when assessing variability explained (mean:  $r^2=0.77$ ; median:  $r^2=0.83$ ;  $n=235$  species) and the ratio of the standard error vs. slope of bark thickness ~ stem diameter relationship (ratio of SE/slope mean: 0.19; median: 0.16;  $n=151$  species). These errors are relatively minor when compared to the differences across biomes (Figure 1, Tables S2-S4).

#### Spatial analyses of grid cell bark thickness means

This involved summarizing traits, fire regimes, and climate conditions within  $1^\circ \times 1^\circ$  grid cells using the GBIF occurrence data. A model without considering different effects in biomes explained less of the variance and had a higher AIC than when considering biome ( $r^2=0.39$  vs.  $r^2=0.57$ ; AIC = 13038 vs. 10865). Consequently, we split the analysis into different biome categories and analyzed savanna and forest species trait means separately to avoid inflating the fire regime of forest species and deflating the fire regime of savanna species in ecotonal areas with high co-occurrence of the two biomes in spatial proximity (e.g. Fig. 1, South America and Australia).



Within biomes, a statistical model of the probability density of community as a function of fire and wet and dry quarter precipitation explained 33% and 35% of deviance in forest and savanna communities, respectively. There were significant non-linear relationships between bark thickness and climate variables (savanna, non-linear AIC: 3023.91, linear AIC: 3584.998; forest, non-linear AIC: 1702.902, linear AIC: 3160.667). These models were then used to project the bark thickness distributions under future conditions.

We also evaluated the potential for spatial autocorrelation affecting the model fit and results. To do so, we calculated the residuals from the model for each gridcell and performed a Moran's I test. We found significant spatial autocorrelation for the savanna ( $p < 0.0001$ ) and forest ( $p < 0.0001$ ) models. To verify our results were robust to potential spatial autocorrelation we (i) compared our model with a model include latitude and longitude as an interactive effect and (ii) used a correlogram to determine the minimum distance for independence and fit the model on repeatedly resampled independent data. To evaluate the robustness of our model, we compared our model's predictions with those of the resampled fittings.

Incorporating latitude and longitude as an interactive effect increased the explanatory power of the model (deviance explained: 68% in savanna and 45% in forests) and produced significantly similar predictions to the model without spatial effects (regression between predicted bark thickness: slope=1.004,  $r^2=0.35$ ,  $p < 0.0001$  in savanna and slope=1.000,  $r^2=0.43$ ,  $p < 0.0001$  in forests). Importantly, the predictions of the spatial distribution of bark thicknesses were qualitatively the same (e.g., savanna fit in Fig. S10).

Repeatedly fitting the model on resampled data sufficiently far apart to allow for independence also reproduced our results. The fitted values from the different re-sampling models ( $n=500$  resample model fits) were significantly related to the global model fits for

savannas and forests: mixed effects model with iteration number as random effect, savannas:  
 $F_{1,4592}=1806$ ,  $p<0.0001$ ; forests:  $F_{1,5605}=13864$ ,  $p<0.0001$ .

### Climate projections

Models included are: BCC-CSM1-1, GFDL-CM3, HadGEM2-ES, MIROC-ESM, NorESM1-M. The model outputs are bias-corrected and calibrated using WorldClim 1.4 at 5-minute resolution. We averaged forecasted values across all models within each grid cell. Future fire projections come from a recent output of LPJ-GUESS-SIMFIRE (Knorr *et al.* 2015), which incorporates future climates, human populations, and fuel loads. The model projects changes in annual burned area to 2071-2100 assuming the RCP8.5 climate scenario. We chose this high emissions scenario to quantify an upper bound on potential changes in fire regimes. Because future fire projections rely on human factors (e.g. population growth, ignition sources, suppression), climate factors (e.g. rainfall, temperature, vapor pressure deficit), and vegetation itself, they inherently contain a large degree of uncertainty in the amount of annual burned area and the areas where it may change the most. Thus, we consider the potential sensitivity of our results to variation in projected climate conditions and examine qualitatively the potential influence of uncertainties in human factors on our findings based on published patterns (Knorr *et al.* 2015). To evaluate uncertainty across climate model projections, we used the standard deviation among climate model precipitation projections (CMIP5 outputs for 2070 RCP8.5 from BCC-CSM1-1, GFDL-CM3, HadGEM2-ES, MIROC-ESM, NorESM1-M.) to calculate “wet” (+1 standard deviation) and “dry” (-1 standard deviation) future scenarios.

### Uncertainties in future projections

773           The model forecasts used here focus on the upper bound scenarios for both changes in  
774 climate (RCP8.5) as well as fire (incorporates a high RCP8.5 scenario as well as high population  
775 growth).

776           Although evaluation of the full variability in future climate and fire projections are out of  
777 the scope of this study, we evaluate uncertainties in our projections within gridcells. We evaluate  
778 the uncertainty by considering uncertainty in the climate projections of wet and dry season  
779 precipitation.

780           To evaluate uncertainty within the climate projections we used the standard deviation in  
781 precipitation among the models (CMIP5 outputs for 2070 RCP8.5 from BCC-CSM1-1, GFDL-  
782 CM3, HadGEM2-ES, MIROC-ESM, NorESM1-M.) to calculate a “wet” scenario by adding one  
783 standard deviation to the mean to for wet and dry season precipitation . Similarly, we calculated  
784 a “dry” scenario by subtracting one standard deviation from the mean.

785           Similarly, because future fire projections rely on human factors (e.g. population growth,  
786 ignition sources, suppression), climate factors (e.g. rainfall, temperature, vapor pressure deficit),  
787 and vegetation itself, they inherently contain a large degree of uncertainty in the amount of  
788 annual burned area and the areas where it may change the most. Thus, we consider the potential  
789 sensitivity of our results by discussing the potential influence that uncertainties in human factors  
790 may have on our findings based on published patterns (Knorr *et al.* 2015).

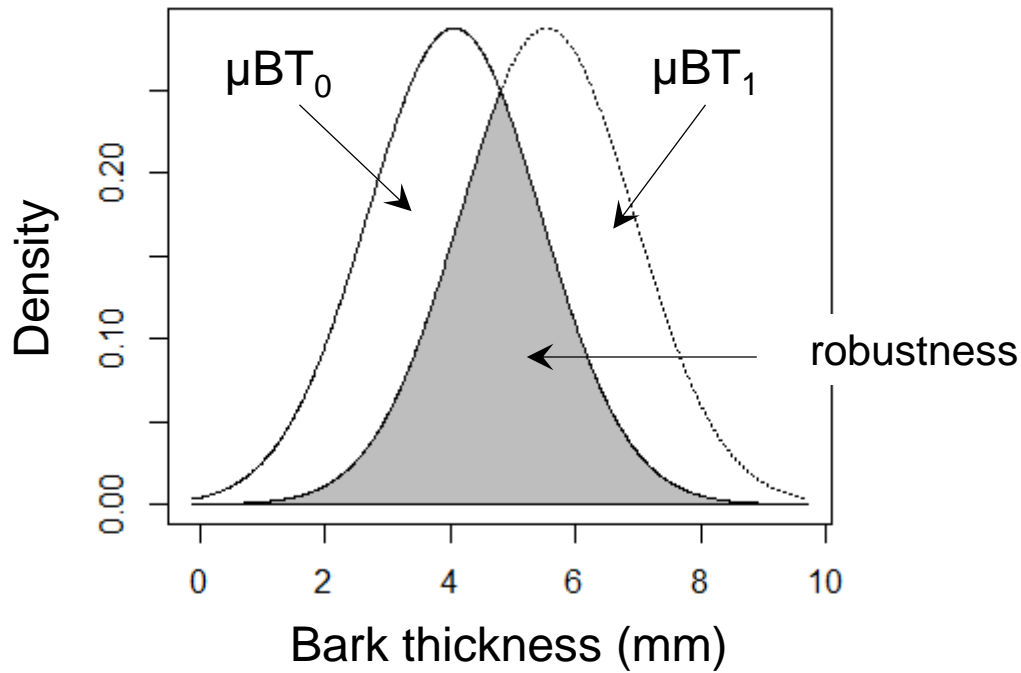
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792 **Figure S1:** Distribution of plant species used in the analysis taken from GBIF and amounting to  
793 578,071 observations. grey indicates areas where the species under consideration do not occur.



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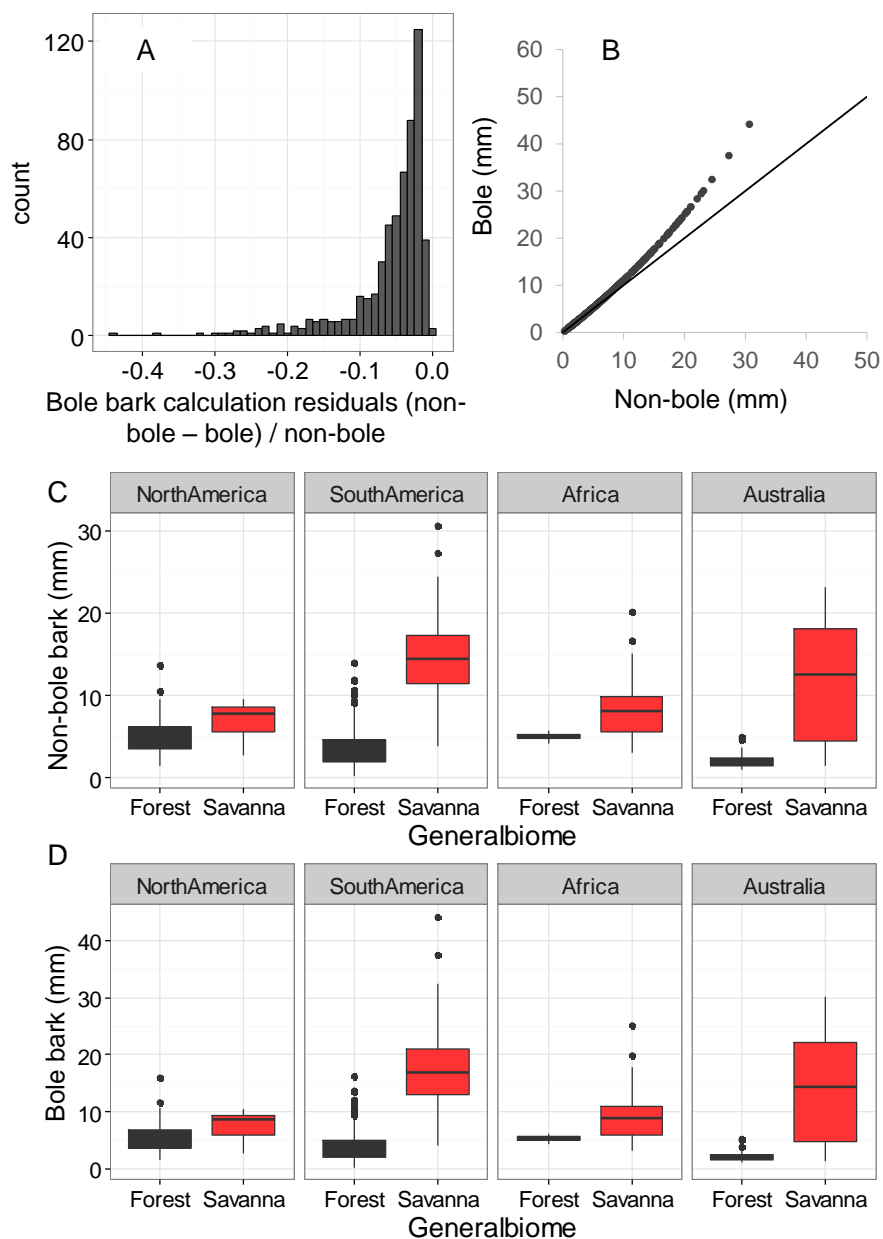
796 **Figure S2:** Schematic representing trait overlap to calculate robustness. Bark thickness  
 797 distributions within a location calculated using present-day means in a grid cell combined with  
 798 total variance in bark thickness. Future means are calculated by integrating projected fire and  
 799 climate into the bark thickness ~ environment model. Variance in bark thickness is assumed  
 800 constant. The integral under overlapping curves is the overlapping coefficient and we interpret it  
 801 here to quantify robustness. Present-day mean bark thickness indicated by  $\mu BT_0$  and future mean  
 802 bark thickness indicated by  $\mu BT_1$ .



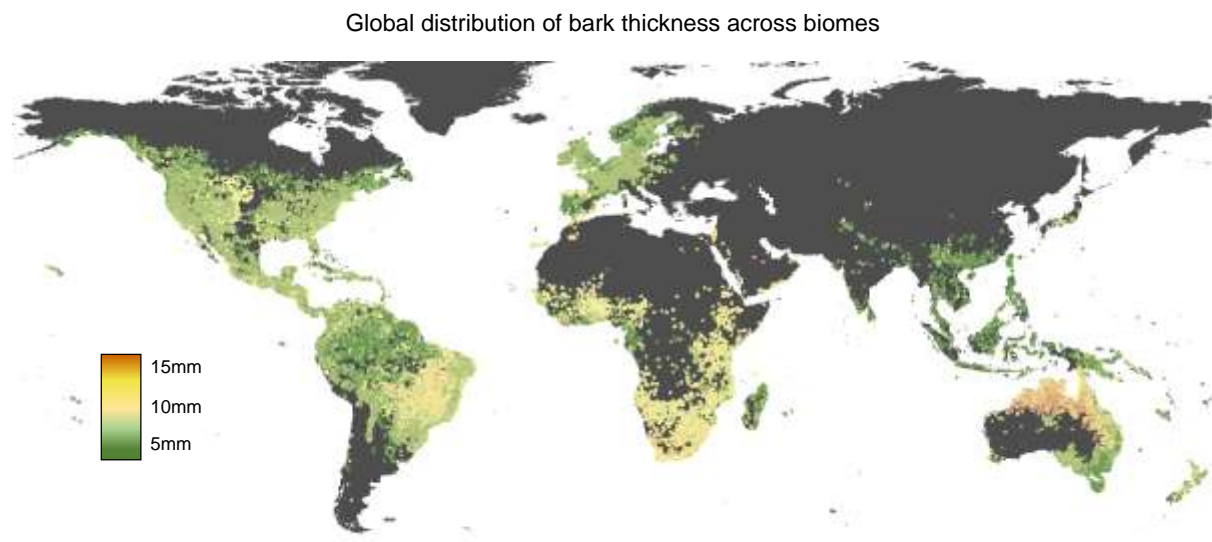
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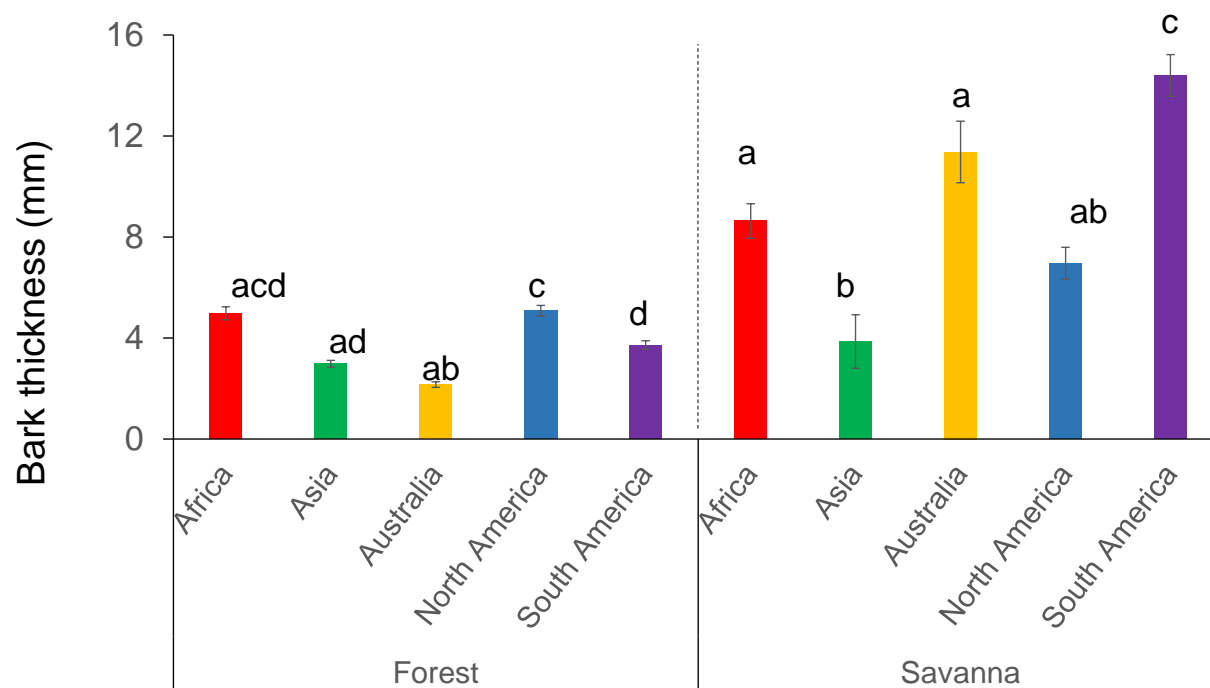
**Figure S3:** Sensitivity of our results to calculations of relative bark thickness based off of outer stem diameter from alternative calculations using the diameter from the stem bole (Midgley & Lawes 2016). All calculations were performed on stem diameters of 10cm. A) histogram of the residuals between the calculation of outer bark (non-bole) vs. bole. B) scatter plot of the two calculation methods with the solid line representing the 1:1 relationship. C and D) comparison between biomes across continents using the two different calculation methods of outer bark (C) and bole (D). Qualitative results using bole calculations were the same (NA:  $F_{1,103}=6.57$ ,  $p=0.0118$ ; SA:  $F_{1,269}=217$ ,  $p<0.0001$ ; AF:  $F_{1,36}=5.15$ ,  $p=0.0294$ ; AU:  $F_{1,91}=144.6$ ,  $p<0.0001$ ).



**Figure S4:** Global distribution of bark thickness across all species. Occurrence points were inverse distance weighted to create spatial averages within distances of 0.5 degrees around each observation point. Bark thicknesses correspond to trees with a reference stem diameter of 10 cm. Grey areas are locations where we do not contain data.

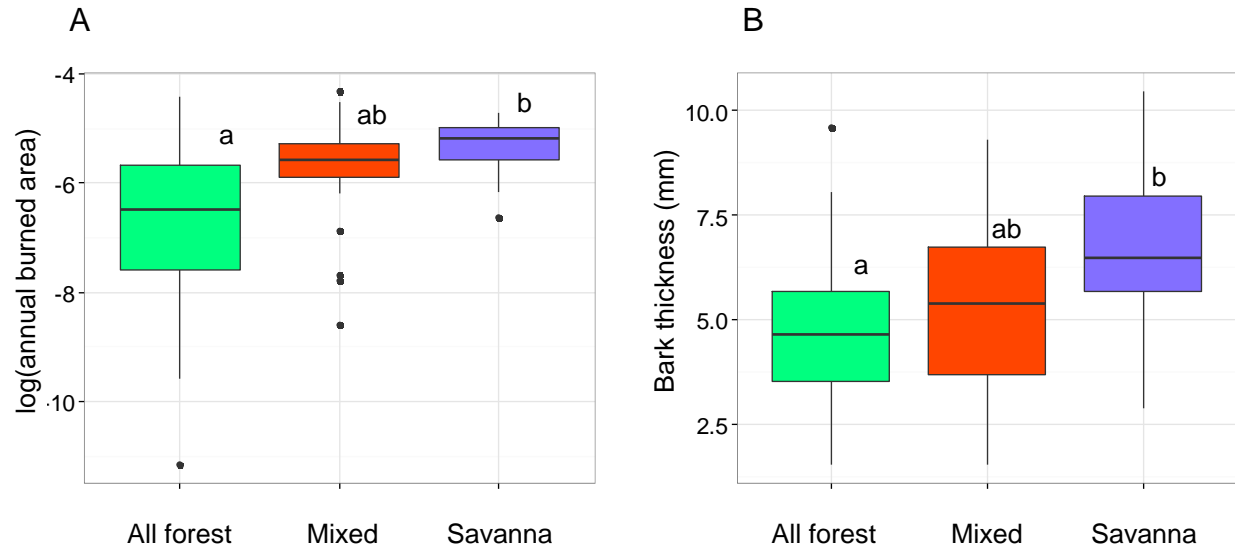


**Figure S5:** Bark thickness of 10cm diameter stems in savanna and forest biomes across continents. Letters indicate significant differences determined via Tukey HSD with correction for multiple comparisons (Table S4 for statistics).

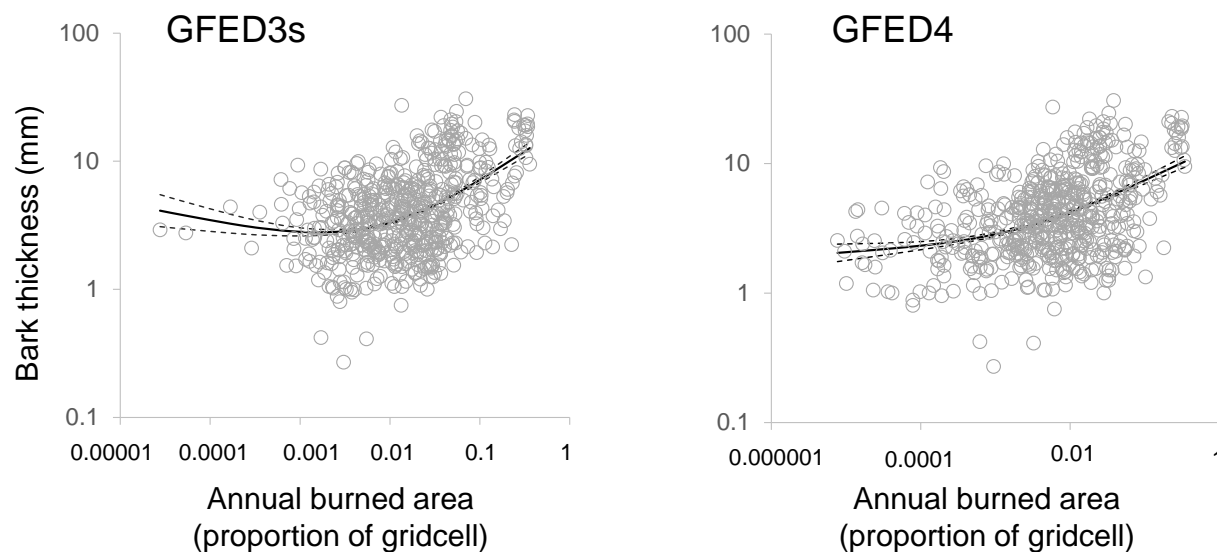




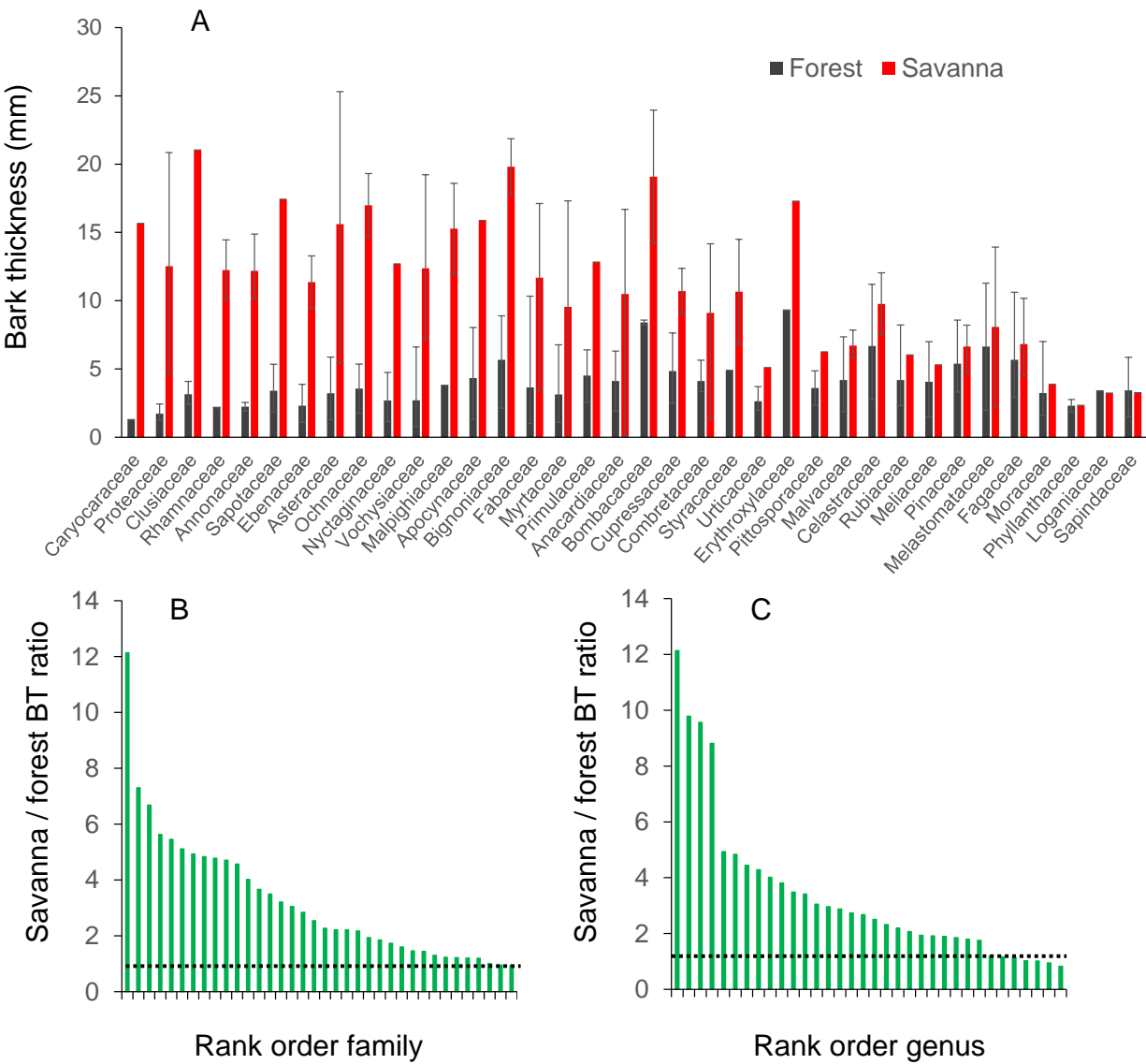
834 **Figure S6:** Annual burned area and bark thickness across species specialized in different habitat  
835 types in North America. Bark thickness is evaluated for a stem 10 cm in diameter. Letters  
836 indicate significant differences among treatments evaluated using a Tukey HSD post-hoc at  
837  $p < 0.05$ .



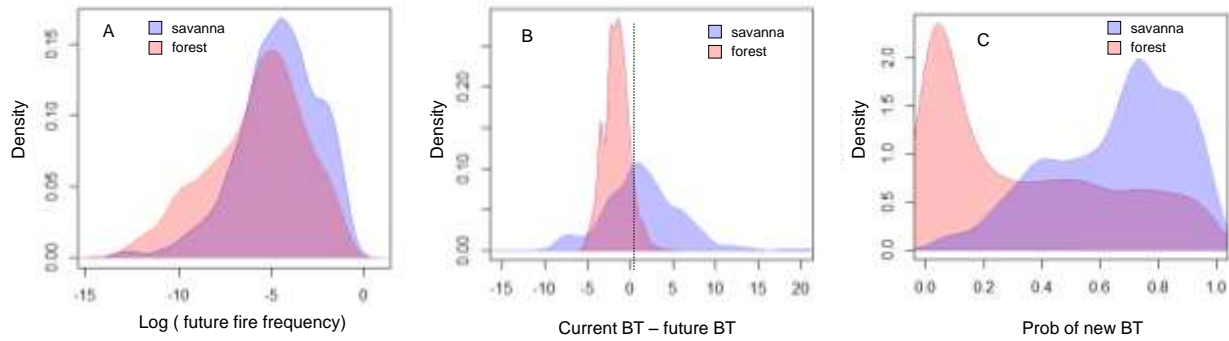
**Figure S7:** Comparison of the relationship between burned area and bark thickness using the two different fire frequency datasets. GFED3s is based off of data from 2001-2010 and includes correction for small fires (20% of deviance explained). GFED4 is based off of data from 1996-2015 but does not include correction for small fires likely leading to the lower-bound x-axis being smaller (20% of deviance explained).



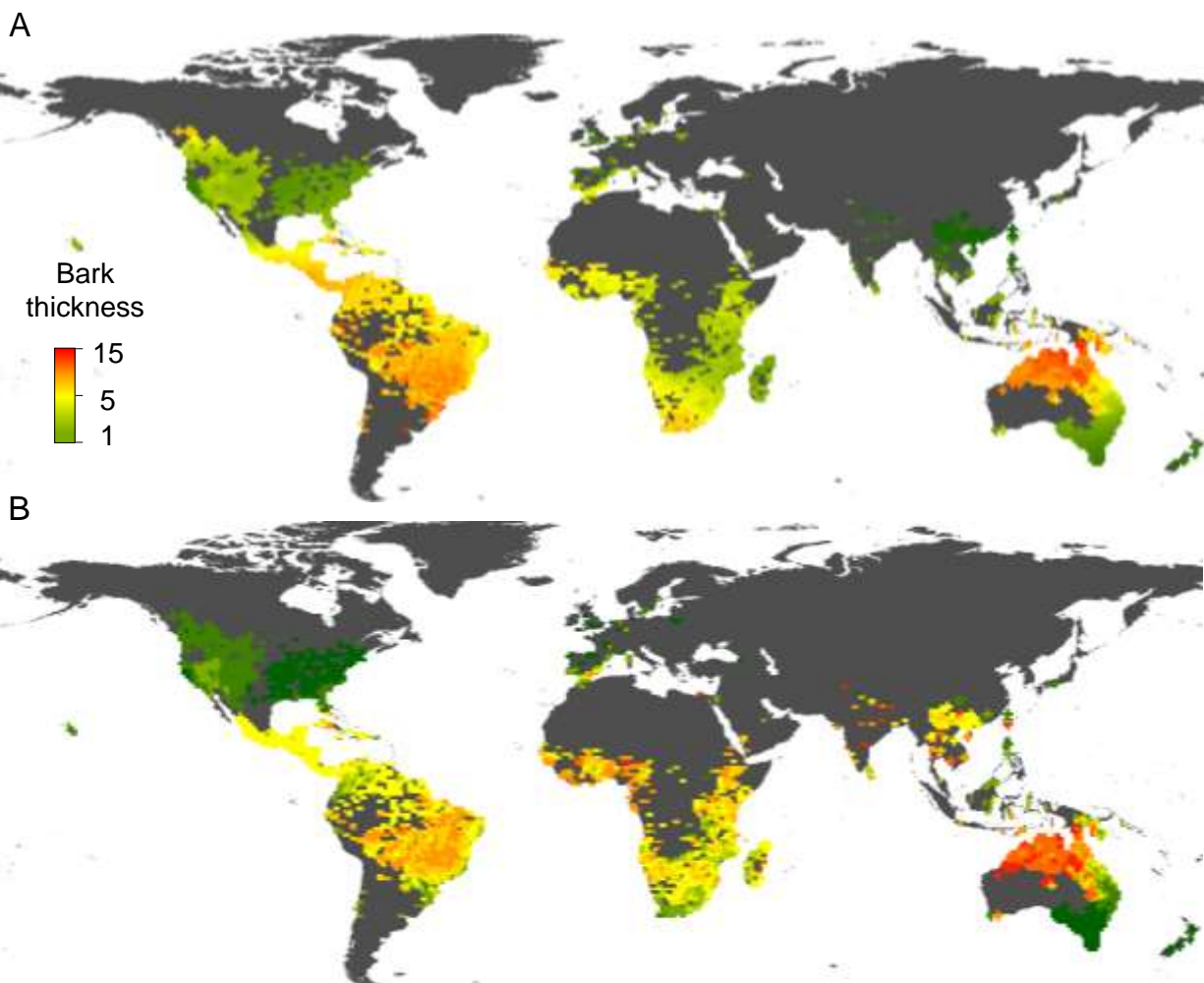
**Figure S8:** A) Comparison of bark thickness in species specializing in savannas vs. forests in the same family. Error bars are  $\pm 95\%$  confidence intervals. Rank order figure illustrates the distribution of bark thickness ratios (savanna / forest) with individual families (B) and genera (C), with the dashed line indicating 1.



**Figure S9:** Future changes in fire and bark thicknesses from modelled projections. A) future annual burned area for grid cells partitioned between savanna vs. forest species. B) absolute changes in bark thickness assuming model projections expressed as probability distributions; C) estimated proportion of individuals in an area containing the new bark thickness (only for cells which are projected to experience increased annual burned area).



864 **Figure S10:** Fitted model output of bark thickness in savannas using a model that either (A)  
865 includes latitude and longitude as model covariates or (B) only includes climate and fire.



866

**Table S1:** List of species, the studies that they were compiled from, their location, biome, and bark thicknesses. The bark thickness for a specific species in some cases came from multiple studies, which we averaged, but present the full dataset for the species available here. **Attached.**

**Table S2:** Means and standard errors of bark thicknesses at particular stem sizes (10, 20, and 30cm) in savanna and forest biomes (both global and across continents). Biome refers to the general biome a species was categorized into and location refers to the geographical grouping. Sample size is given for the 10cm comparison.

Biome	Location	# species	10cm mean	SE	20cm mean	SE	30cm mean	SE
Forest	Global	445	3.71	0.11	6.94	0.20	10.34	0.33
	Tropical	329	3.42	0.12	6.46	0.24	9.43	0.36
	Temperate	116	4.52	0.21	8.29	0.35	13.09	0.74
Savanna	Global	127	11.10	0.54	21.56	1.11	33.50	1.74
	Tropical	110	11.80	0.58	23.20	1.20	34.53	1.83
	Temperate	17	6.22	0.51	10.95	0.88	26.44	5.29
Forest	Africa	5	4.98	0.26	7.49	0.45	10.01	0.81
	Asia	60	2.97	0.14	5.72	0.27	8.43	0.42
	Australia	60	2.16	0.11	4.31	0.22	6.47	0.33
	North America	94	5.08	0.22	9.23	0.36	14.78	0.83
	South America	226	3.72	0.17	6.99	0.33	10.18	0.49
Savanna	Africa	33	8.64	0.68	15.91	1.48	22.99	2.31
	Asia	5	3.85	1.06	7.71	2.12	11.56	3.19
	Australia	33	11.37	1.22	22.74	2.44	34.11	3.66
	North America	11	6.96	0.63	11.63	1.21	33.56	7.60
	South America	45	14.40	0.82	28.80	1.65	43.20	2.47

**Table S3:** Statistical analyses comparing the effect of biome both globally and within continents. All models have log transformed bark thicknesses. Significance of including continent into biome model indicated by the “+” inclusions.

		<u>10cm</u>		<u>20cm</u>		<u>30cm</u>	
	Df	F	p	F	p	F	p
Biome	1,570	313	<0.0001	321	<0.0001	322	<0.0001
+Continent	4,562	18.8	<0.0001	15.2	<0.0001	20	<0.0001
+Continent:Biome	4,562	15.6	<0.0001	17.3	<0.0001	9.7	<0.0001
Biome - Asia	1,63	1.03	0.31	1.5	0.22	1.71	0.19
Biome - Africa	1,36	5.22	0.028	6.21	0.017	5.8	0.021
Biome - Australia	1,92	149	<0.0001	149	<0.0001	149	<0.0001
Biome - North America	1,107	7.78	0.006	4.8	0.031	24.4	<0.0001
Biome - South America	1,287	194	<0.0001	211	<0.0001	215	<0.0001

**Table S4:** Bark thickness differences among continents. Comparison among biomes using Tukey HSD post-hoc test performed separately within each biome. Difference refers to the difference between means (statistics performed on log transformed bark thickness data for 10cm stems).

Comparison	<u>Forest</u>		<u>Savanna</u>	
	<u>Diff</u>	<u>p value</u>	<u>Diff</u>	<u>p value</u>
Asia-Africa	-0.57	0.178	-0.86	0.014
Australia-Africa	-0.90	0.004	0.11	0.923
NorthAmerica-Africa	-0.06	0.999	-0.18	0.895
SouthAmerica-Africa	-0.50	0.270	0.53	<0.001
Australia-Asia	-0.34	0.008	0.97	0.004
NorthAmerica-Asia	0.50	<0.001	0.68	0.160
SouthAmerica-Asia	0.07	0.910	1.38	<0.001
NorthAmerica-Australia	0.84	<0.001	-0.29	0.574
SouthAmerica-Australia	0.41	<0.001	0.41	0.014
SouthAmerica-NorthAmerica	-0.44	<0.001	0.70	0.003



**Table S5:** Statistical results from generalized additive models between log bark thickness, fire, climate, and biome using model selection on stems 20cm and 30cm in size. Dev refers to percent deviance explained. The best fit models are highlighted in bold, we utilized the most parsimonious of the two.

<u>Variables included</u>	AIC 20cm	Dev 20cm	AIC 30cm	Dev 30cm
<b>Mean_fire+Precip_Wetq*Biome+Precip_Dryq*Biome</b>	940	49.7%	993	48.0%
<b>Mean_fire+Precip_Wetq*Biome+Precip_Dryq</b>	941	49.4%	991	48.0%
Mean_fire+Precip_Wetq+Precip_Dryq*Biome	976	46.2%	1027	45.2%
Mean_fire+Precip_Wetq+Precip_Dryq+Biome	980	45.8%	1026	44.5%
Precip_Wetq+Precip_Dryq+Biome	980	45.5%	1024	44.4%
Mean_fire+Precip_Dryq+Biome	988	42.3%	1033	43.5%
Mean_fire+Precip_Wetq+Biome	1014	39.9%	1056	41.3%
Mean_fire+Biome	1053	38.1%	1091	37.4%
Biome	1068	36.0%	1096	36.5%
Mean_fire+Precip_Wetq+Precip_Dryq	1088	34.3%	1147	31.2%
Mean_fire	1189	21.1%	1240	18.1%

**Table S6: Using GFED4 to characterize environmental conditions that determine bark thickness.** Statistical results from generalized additive models between log bark thickness (for stems 10cm in size), fire, climate, and biome using model selection. Dev refers to deviance explained. Mean\_fire = annual burned area, **Precip\_Wetq** = precipitation in the wettest quarter, **Precip\_Dryq** = precipitation in the driest quarter, Biome = biome a species specialized in (either savanna or forest). The best fit models are highlighted in bold, we utilized the more parsimonious of the two.

<u>Variables included</u>	<u>Dev</u>	<u>AIC</u>
<b>Mean_fire+Precip_Wetq*Biome+Precip_Dryq*Biome</b>	<b>49.8%</b>	784.654
<b>Mean_fire+Precip_Wetq*Biome+Precip_Dryq</b>	<b>49.6%</b>	785.1415
Mean_fire+Precip_Wetq+Precip_Dryq*Biome	47.2%	807.0707
Mean_fire+Precip_Wetq+Precip_Dryq+Biome	46.6%	809.7317
Precip_Wetq+Precip_Dryq+Biome	46.6%	810.6547
Mean_fire+Precip_Dryq+Biome	45.1%	823.489
Mean_fire+Precip_Wetq+Biome	43.3%	838.3743
Mean_fire+Biome	39.2%	869.499
Biome	36.5%	888.4946
Mean_fire+Precip_Wetq+Precip_Dryq	33.0%	916.2993
Mean_fire	19.2%	1001.298

**Table S7: Using GFED4 to characterize environmental conditions that determine bark thickness.** Statistical results from generalized additive models between log bark thickness, fire, climate, and biome using model selection on stems 20cm and 30cm in size. Dev refers to percent deviance explained. The best fit models are highlighted in bold, we utilized the most parsimonious of the two.

<u>Variables included</u>	AIC 20cm	Dev 20cm	AIC 30cm	Dev 30cm
<b>Mean_fire+Precip_Wetq*Biome+Precip_Dryq*Biome</b>	<b>789.79</b>	<b>49.4%</b>	997.90	47.5%
<b>Mean_fire+Precip_Wetq*Biome+Precip_Dryq</b>	<b>790.30</b>	<b>49.2%</b>	998.88	47.5%
Mean_fire+Precip_Wetq+Precip_Dryq*Biome	815.84	46.4%	1032.13	44.0%
Mean_fire+Precip_Wetq+Precip_Dryq+Biome	817.92	45.9%	1033.71	44.0%
Precip_Wetq+Precip_Dryq+Biome	819.6	45.8%	1035.67	43.9%
Mean_fire+Precip_Dryq+Biome	826.09	45.0%	1040.80	43.2%
Mean_fire+Precip_Wetq+Biome	849.79	42.1%	1060.54	41.2%
Mean_fire+Biome	870.78	39.3%	1082.00	38.8%
Biome	885.32	37.2%	1095.02	37.2%
Mean_fire+Precip_Wetq+Precip_Dryq	931.79	31.0%	1165.29	29.2%
Mean_fire	1007.84	18.4%	1253.13	17.0%

**Table S8: Analysis within North America.** Statistical results from generalized additive models between log bark thickness (for stems 10cm in size), fire, climate, and biome using model selection. Dev refers to deviance explained. Mean\_fire = annual burned area, Precip\_Wetq = precipitation in the wettest quarter, Precip\_Dryq = precipitation in the driest quarter, Biome = biome a species specialized in (either savanna or forest). The best fit models are highlighted in bold, we utilized the more parsimonious of the two.

<u>Variables included</u>	<u>Dev</u>	<u>AIC</u>
<b>Mean_fire+Precip_Wetq+Precip_Dryq</b>	<b>17.40%</b>	<b>110.6098</b>
<b>Mean_fire+Precip_Dryq+Biome</b>	<b>19.70%</b>	<b>111.6916</b>
Mean_fire+Precip_Wetq+Precip_Dryq+Biome	20.30%	112.8949
Mean_fire+Precip_Wetq*Biome+Precip_Dryq	22.60%	115.8903
Mean_fire+Precip_Wetq+Precip_Dryq*Biome	21.20%	117.6691
Mean_fire	7.57%	118.1583
Mean_fire+Biome	11.20%	119.9901
Mean_fire+Precip_Wetq*Biome+Precip_Dryq*Biome	23.50%	120.6815
Mean_fire+Precip_Wetq+Biome	11.30%	121.9151
Biome	7.57%	122.1543
Precip_Wetq+Precip_Dryq+Biome	9.33%	124.1714